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THE LOCATION OF MONARCH BUTTERFLY (*DANAUS PLEXIPPUS* L.) OVERWINTERING COLONIES IN MEXICO IN RELATION TO TOPOGRAPHY AND CLIMATE

William H. Calvert and Lincoln P. Brower

Department of Zoology, University of Florida,
Gainesville, Florida 32611

ABSTRACT. Each year monarch butterflies migrate from breeding grounds in the United States and Canada to the Transvolcanic Belt of central Mexico. Here, within the montane fir forests, they initially aggregate in small groups of loose clusters scattered along high ridge crests. During November and December the numerous small groups consolidate into a few large compact aggregations and move downward into more protected positions closer to water. Butterfly activity increases in the last half of February due to seasonal warming. The consolidation and compaction processes that marked the beginning of the season reverse, and the colonies spread out and often split into two or more parts. After mid-March, colony size decreases as the butterflies begin to remigrate northward. Several characteristics of the climate and physiography of the Transvolcanic Belt, including moisture, altitude, and slope exposure and inclination, are important to the overwintering biology of the monarch butterfly. The forests of the zone play a major role in satisfying the overwintering monarchs' microclimatic requirements by moderating temperature extremes and conserving moisture. By colonizing this high altitude area in the tropics, the butterflies appear to satisfy microclimatic requirements that include temperatures low enough to keep activity, metabolism, and lipid expenditure to a minimum, but not so cold as to cause freezing; sufficient solar input to allow thermoregulatory basking and consequent flight; and sources of moisture and nectar.

Each autumn, millions of monarch butterflies (*Danaus plexippus* L.) migrate southwest or south (Urquhart & Urquhart 1978, Schmidt-Koenig 1979) from breeding grounds in eastern and central United States and southern Canada to overwintering sites in Mexico. Funneling through Texas, they cross into Mexico and encounter the southern extension of the Rocky Mountains, the Sierra Madre Oriental. Here they change their southwesterly course and follow the ranges to the southeast, eventually cross them, and continue to the Transvolcanic Belt, the volcanic mountains that extend across the southern end of Mexico's Central Plateau (Altiplanicie Mexicana) between 19° and 20°N latitude. At a few isolated places within the high altitude coniferous forests, which are scattered through this belt of mountains (Fig. 1), monarchs spend the winter in aggregations estimated to be in the tens of millions (Brower et al. 1977, Calvert, in prep.).

Monarchs migrate south in the fall to avoid winter cold and survive in cool, moist places where they can conserve fuel reserves in a state of reproductive inactivity until making the return trip north in the spring. Yet weather in the overwintering areas does not ideally meet monarch requirements. Not only do temperatures occasionally fall into the lethal range (Calvert et al. 1983), but also intense insolation on clear and partly cloudy days stimulates butterfly activity to an extent that appears to contradict their need to conserve fuel. In an attempt to resolve these apparent contradictions, and to understand better why the monarchs choose these particular areas in Mexico, we here describe characteristics of the annual overwintering cycle and ecological features of several overwintering areas that we studied for nine seasons (December 1976 through spring 1985).

PHYSIOGRAPHIC FEATURES, CLIMATE AND VEGETATION

Volcanic cones and ranges dominate the terrain of the Transvolcanic Belt, which has an area of 60,000 km^2, and measures approximately 640 km across by 95 km wide (Moore 1945). To the north it is bounded by the high Mexican plateau, and on the south by the large Balsas River drainage (Rzedowski 1978). Its eastern portion averages 2200 m elevation with numerous peaks rising above 3600 m, including the highest mountains in North America south of Alaska (Goldman 1951). The western portion contains fewer high peaks, and declines in elevation towards the Pacific. The central area where the monarch colonies are located (Fig. 1) is drained to the north and east by the Rio Lerma and to the south and west by the Balsas-Mezcala river system (Arbingast et al. 1975).

Classic wet-dry season weather patterns prevail through most of the Transvolcanic Belt. Precipitation and heavy clouding is frequent from May until October, especially in the mountains, but winters are dry, and arid conditions prevail on the interior plains (Goldman & Moore 1945). However, winter and early spring storms occasionally occur in the area, and the higher elevations are subjected to high winds, heavy rains, snow, and ice storms (Mosina-Aleman & Garcia 1974). While potentially lethal to the overwintering butterflies (Calvert et al. 1983), these storms are also beneficial because they reduce the severity of the winter drought in the high-elevation overwintering areas.

Because of the wide range of altitudes and climatic conditions, vegetation within the Transvolcanic biotic province is extremely varied. High interior plains and valleys consist largely of grasslands intermixed with patches of small trees, shrubs, yuccas, agaves and cacti. On mountainous slopes, forests dominated by oaks and pines give way to firs at about 2750 m (Goldman 1951), but in more humid areas, the firs commence as low as 2400 m (Rzedowski 1978). On the highest peaks, firs give way to alders and other species of pine and eventually to grassland and tundra (Goldman 1951, Goldman & Moore 1945). As is true of the lower limits, vegetational transitions depend on moisture and exposure, and the altitudinal limits of the fir zone may be influ-

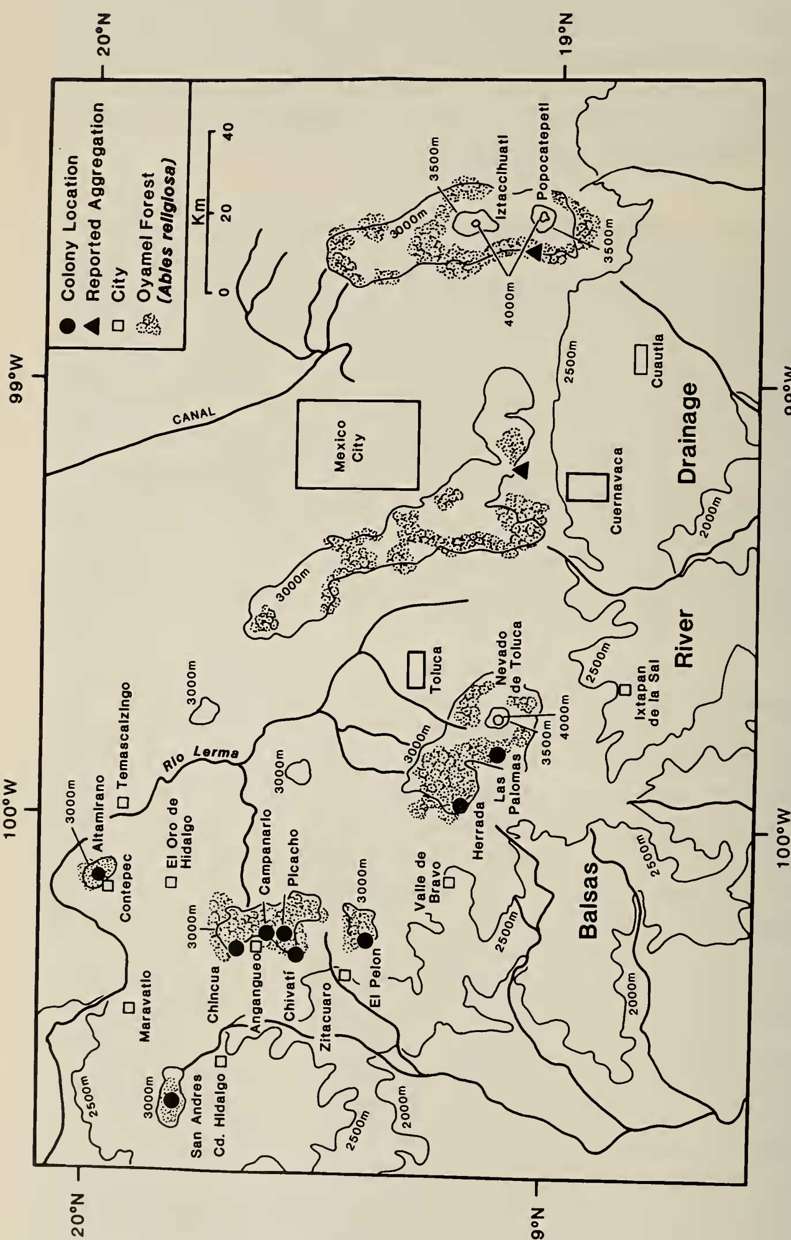

FIG. 1. Location of monarch butterfly overwintering areas in relation to topography, drainage patterns and oyamel (*Abies religiosa*) forests of Mexico's Transvolcanic Belt. Names of colonies are underlined and distribution of the oyamel forests is based on Anon. (1981). Contour interval = 500 m.

TABLE 1. Physical characteristics of 30 monarch overwintering colonies in Mexico, 1976–1982.

No.	Colony name	Date mapped	Size (ha)	Altitude (m)	Slope declination	Facing azimuth	Approximate location
				1976/77			
1	Chincua[1] 1	27 Jan	1.50	3,085	26°00′	360°	Slope of Arroyo Zapatero, Sierra Chincua, Michoacan (19°41′N, 100°18′W)
				1977/78			
2	Chincua 1	15 Jan	0.37	3,067	26°20′	4°	Slope of Arroyo Zapatero, Sierra Chincua
		2 Feb	0.76			339°	
3	Chincua 2	16 Feb	2.62	3,134	28°50′	310°	Slope of Arroyo La Plancha, Sierra Chincua
		30 Mar	0.78				Bottom of same
4	Altamirano[2]	27 Nov	0.69	3,152	26°30′	262°	Slope of Cerro Altamirano, near Contepec, Michoacan (19°58′N, 100°08′W)
		14 Feb	0.46				
5	Pelon[3]	31 Jan	1.47	3,000	18°40′	351°	Shallow canyon on Cerro Pelon, near Donato Guerra, Mexico (19°23′N, 100°16′W)
6	Herrada[4]	24 Jan	0.25	3,153	21°30′	212°	Slope of Cerro Piedra Herrada, near Valle de Bravo, Mexico (19°11′N, 99°57′W)
				1978/79			
7	Chincua 1	6 Dec	1.49	3,342	13°30′	132°	Slope of Rincon Villalobos
		11 Jan	—	3,321	20°10′	236°	Arroyo La Plancha, Sierra Chincua
8	Chincua 2	4 Nov	0.16	3,260	29°30′	193°	Slope of Arroyo La Plancha, Sierra Chincua
		12 Nov	0.53	—	—	—	
9	Chincua 3	6 Dec	0.10	3,280	29°00′	220°	Slope of Arroyo La Plancha, Sierra Chincua
10	Chincua 4	15 Nov	2.51	3,180	16°10′	230°	Slope of Arroyo Zapatero, Sierra Chincua
		13 Dec	3.29	—	—	—	
		15 Jan	2.25	—	—	—	
		9 Feb	2.25	3,134	—	—	
		3 Mar	2.72	—	—	—	Bottom of Arroyo Zapatero
		22 Mar	3.20	—	—	—	
		15 Apr	0.00	—	—	—	Colony remigrated to north

TABLE 1. Continued.

No.	Colony name	Date mapped	Size (ha)	Altitude (m)	Slope declination	Facing azimuth	Approximate location
11	Chincua 5	15 Nov	0.05	—	—	—	Upper slope of Arroyo La Plancha, Sierra Chincua
12	Chincua 6	15 Nov	0.09	—	—	—	Upper slope of Arroyo La Plancha, Sierra Chincua
13	Altamirano	14 Dec	0.19	3,200	26°30′	244°	Slope of Cerro Altamirano, near Contepec, Michoacan
1979/80							
14	Chincua 1	9 Nov	1.20	3,290	30°00′	201°	Upper slope of Arroyo La Plancha, Sierra Chincua
		6 Jan	0.43	—	—	—	
		27 Jan	0.03	—	—	—	
15	Chincua 2	9 Nov	0.33	3,159	33°20′	219°	Upper slope of Arroyo La Plancha
		9 Jan	0.21	—	—	—	
		18 Jan	0.10	—	—	—	
16	Chincua 3	18 Jan	0.25	3,251	37°10′	218°	Upper slope of Arroyo La Plancha
17	Chincua 4	17 Jan	0.54	2,928	14°00′	239°	Bottom of Arroyo La Plancha, derived from colonies 14–16
18	San Andres	3 Dec	0.19	3,120	20°10′	207°	Slope of Cerro San Andres, near Los Asufres, Michoacan (19°47′N, 100°36′W)
1980/81							
19	Chincua 1	22 Nov	0.92	3,155	35°40′	204°	Slope of Arroyo La Plancha, Sierra Chincua
20	Chincua 2	22 Nov	0.13	3,122	15°30′	242°	Slope of Arroyo La Plancha, Sierra Chincua
21	Chincua 3	22 Nov	0.03	3,290	25°00′	190°	Slope of Arroyo La Plancha, Sierra Chincua
22	Chincua 4	29 Nov	0.32	3,357	28°40′	179°	Slope of Arroyo La Plancha, Sierra Chincua
23	Chincua 5	30 Nov	0.12	3,171	31°40′	191°	Slope of Arroyo La Plancha, Sierra Chincua
24	Chincua 6	3 Dec	0.49	3,054	13°40′	261°	Shallow slope near bottom of Arroyo Zapatero, Sierra Chincua
		8 Jan	0.65	—	—	—	

TABLE 1. Continued.

No.	Colony name	Date mapped	Size (ha)	Altitude (m)	Slope declination	Facing azimuth	Approximate location
		8 Feb	0.60	—	—	—	
		8 Mar	—	3,019	—	—	
25	Chincua 7	11 Jan	2.51	3,000	31°00′	120°	Near bottom of Arroyo La Plancha
26	Acuña	15 Jan	—	3,400	0°00′	—	Mountain SE of Cerro Los Capulines, Sierra Rancho Grande, Michoacan, local name is Acuña (19°39′N, 100°15′W)
				1981/82			
27	Chincua	8 Feb	1.47	2,971	35°40′	150°	Slope of Arroyo La Plancha
28	Picacho 1	6 Mar	2.03	3,135	17°50′	325°	Headwaters of Arroyo La Hacienda, Sierra El Campanario, near Ocampo, Michoacan (19°35′N, 100°15′W)
29	Campanario	6 Mar	3.34	3,178	24°10′	229°	Slope of Arroyo Los Conejos, Sierra El Campanario, near Ocampo (19°00′N, 100°00′W)
30	Chivatí	7 Mar	0.20	3,098	17°50′	134°	Slope of Cerro Chivatí, near Ocampo, Michoacan (19°32′N, 100°18′W)
Mean[5]			0.85	3,158	25°22′	230°18′	
SD or Angular confidence interval			0.94	118	1°	28°	

[1] The original Site Alpha area (Brower et al. 1977).
[2] The original Site Beta area (Calvert et al. 1979).
[3] The original Site Gamma area (Calvert et al. 1979).
[4] The original Site Delta area (Calvert et al. 1979).
[5] Where more than one measurement was taken, that closest to 1 February (the middle of the stable period) was chosen to compute the means and standard deviations.

enced by the presence and extent of the summer fog belt (review in Brower 1985).

HISTORY OF THE OCCURRENCE OF OVERWINTERING COLONIES

Residents of settlements located near overwintering colonies in the Sierra Chincua, Michoacan, claim that monarchs have always come to these areas. Although butterfly motifs occur widely in Precolumbian art and mythology (Brewer 1983), especially in the Teotihuacan culture (Castellanos 1983, de la Maza 1976), we have not found mention of monarch colonies in the literature prior to Urquhart's original report (1976). Lack of Precolumbian records of the conspicuous overwintering phenomenon may be due in part to its location near the boundaries of the Tarascan and Aztec empires (West 1964), which may well have been a dangerous no man's land. Possible folk-knowledge of monarchs may be expressed in the frequent use of the local Spanish name for butterfly, "paloma," in topographic features both in the overwintering areas and in areas through which they migrate. The migratory phenomenon has also found its way into the language of the Mazahua, a group of Indians living in the migratory corridor in the village of Santiago north of Villa Victoria, in the state of Mexico. Their word, "šeperito," translates as "butterfly that passes in October and November" (Kiemele Muro 1975). Historically, monarchs may have been important to the Mazahua as a supplemental food source. Collecting them at temporary roosts during the fall migration, Mazahuas still eat monarchs after removing the wings and frying them on flat ceramic pans (comals). However, the practice is now apparently limited to occasional performances for tourists (Yamaguchi 1980).

METHODS

We here depart from procedures in our previous report (Calvert et al. 1979) and name the colonies according to the mountain peak or range on which they are located. In cases where two or more colonies occupied the same peak or range in the same year, a number follows the name and signifies a specific colony location with the peak or range. Site Alpha, originally described in Brower et al. (1977), was located in the Sierra Chincua and is now called the Chincua overwintering area. Place names, geographical features and coordinates (Table 1) were determined from the Mexican CETENAL map series (Anon. 1976a).

Between December 1976 and March 1982 we spent a total of 19 months at various colonies in the Transvolcanic Belt including 94 days during 1978–79 at Chincua 4 in the state of Michoacan. During this time we located 30 colonies on 5 mountain massifs and mapped each using a Suunto sighting compass and a 100 m surveying tape. Colony area was computed using a Hewlett-Packard double meridian distance program or an Apple II graphics program. Colony boundaries were marked with date-coded colored tape to monitor changes in positions. We recorded the declination of the mountain slope at the position of the colony and the "facing azimuth," that is, the direction of the down-slope line perpendicular to the contour at the colony center. To determine significance and angular confidence interval of the average facing azimuth, we applied circular statistics (Batschelet 1972) to azimuths, corrected for magnetic declination, approximately 8.5° east (Anon. 1976a). Circular statistics were also used to derive the angular confidence interval for the average slope declination.

During 1978–79, daily temperatures were monitored continuously from 19 January–24 March with recording hygrothermographs (Brower & Calvert 1985) at two locations, one in the forested center of Chincua 4 (Colony #10, Table 1) and the other in a nearby clearing. Forest and understory plants were identified at the University of Texas Lundell Herbarium, or by reference to Sanchez (1979).

RESULTS AND DISCUSSION

Location of Colonies

The 30 colonies we found were located in the high-altitude mountainous terrain of the Mexican Transvolcanic Belt between 19°10′ and 20°00′N latitude and 99°55′ and 100°40′W longitude (Table 1), a rectangle of about 7000 km² (Fig. 1). Evidence of other colonies, indicated by the presence of detached wings and body parts spread over areas up to 0.25 ha, occurred as far east as 99°52′ near the volcano Nevado de Toluca. (A small colony indicated as Los Palomas in Fig. 1 was discovered here in November 1984.) Small overwintering aggregations confined to one or a few trees have been reported east of Mexico City on the western slopes of the volcanoes Popocatepetl and Ixtaccihuatl (98°45′W; J. de la Maza, pers. comm.) and south of Mexico City in the vicinity of Tres Marias (99°10′W; J. Mausan, pers. comm.). These small aggregations appear to be outlying groups that do not form every year, and no mass movement of migrant butterflies into these areas has been observed or reported.

Several locations outside the Transvolcanic Belt, and in its eastern extreme, appear to have habitat characteristics and the requisite altitude to be suitable for monarch colonies. Monarchs occasionally are seen in migration towards areas removed from known colonies. For example, in October 1980, we saw large numbers migrating SE along the escarpment above Orizaba, Veracruz, apparently headed to the Sierra de Juarez, Oaxaca. In 1977 another group was observed far from known overwintering areas and migratory pathways flying ESE near

Candelaria Loxicha, Oaxaca (de la Maza et al. 1977). Accordingly, we searched in several mountain ranges outside the known overwintering areas, including the western slopes of the Cerro Peña Nevada in the Sierra Madre Oriental, state of Nuevo Leon, in December 1977, and the western slopes of the Cofre de Perote and the Pico de Orizaba, in the states of Puebla and Veracruz in February 1980. In February 1982, our group, including Javier de la Maza of the Mexican Department of Wildlife, investigated several areas in the Sierra de Juarez and the Sierra Madre del Sur, all in the state of Oaxaca. De la Maza returned to these areas in March and early April of the same year and explored further south in the Sierra de Chiapas, eventually reaching the mountainous border of Guatemala. No colonies or evidence of colonies (such as large numbers of dismembered wings) were found.

Unless further data are forthcoming, we conclude that the principal overwintering colonies of the eastern population of the North American monarch (Fig. 1: Pelon, Chivati, Picacho, Campanario, and Chincua) occur on a few isolated mountain ranges confined to a remarkably small area of approximately 800 km² between 19°20′ and 19°45′N latitude and 100°10′ and 100°20′W longitude (at this longitude 1° of latitude = 111 km and 1° of longitude = 104 km). Scattered aggregations, such as colonies Altamirano, Herrada and San Andres (Table 1) are found outside this area, but these are always small, do not form every year, and break up earlier than those in the central area.

Colony Vegetation

Most places in the Transvolcanic Belt between 2500 and 3500 m elevation are dominated by the "oyamel" fir (*Abies religiosa* H.B.K.), which occurs on all terrain except rocky outcroppings and areas of cold air drainage (llanos). This is the major species upon which monarchs form their overwintering roosts. Other trees in the community include *Pinus pseudostrobus* Lindl. (referred to as *Pinus ayacahuite* in Brower et al. 1977), *Cupressus lindleii* Klotzsch, several species of *Quercus*, and *Buddleia cordata* H.B.K. (the last species is confined to moist canyon bottoms). *Cupressus lindleii* is found in dense stands at lower elevations within *Abies religiosa* forests, while *Pinus pseudostrobus* and *Quercus* spp. are more scattered and appear as occasional individuals within the *Abies* forest. Monarchs occasionally roost on all of these tree species but, since they mostly locate their colonies in oyamel-dominated forests, they are usually found on the oyamels. Moreover, when used as roosting trees, the broadleafed angiosperms are generally not covered as densely as are the conifers (Brower et al. 1977).

The most conspicuous components of the forest understory include tall (4 m) and medium (2 m) woody shrubs, dominated by composites, the most important of which are *Senecio anquilifolius* D.C., *S. barba-Johannis* D.C., *Eupatorium mairetianum* D.C. and *E. patzcuarense* H.B.K. Important noncomposites in this portion of the understory are *Cestrum anagyris* Dun., *Salvia elegans* Vahl. and *S. cardinalis* H.B.K. Ground cover is dominated by *Alchemilla procumbens* Rose and one or more species of mosses in the genera *Thuidium* and *Mnium*. Local clearings contain *Senecio stoechadiformis* D.C., *S. tolucanus* D.C., *S. prenanthoides* A. Rich., *S. sanquisorbae* D.C., *Eupatorium* sp. and *Baccharis conferta* H.B.K. All of the species above, except *Alchemilla procumbens,* the *Salvia,* and the mosses, serve as monarch nectar sources at some time in the overwintering period. They also serve as substrates for drinking dew, especially in November and December.

Human disturbance is common in these forests. Lumbering without clearcutting has been practiced for many years in all overwintering areas, and many forest fires have occurred, attributable to lightning, human carelessness and, in some areas, to the practice of renewing and extending pastures. Tree densities range from over 1000/ha in young stands to about 150/ha in severely thinned forests (Calvert et al. 1982).

Colony Formation and Movement

In the Sierra Chincua, we observed colonies forming only within a narrow time range, from 2–9 November. Local foresters near the Sierra El Campanario report that butterfly arrival may vary among years by as much as two weeks and that they have arrived as early as the third week of October (P. Silva, pers. comm.). Initially, the monarchs aggregate in numerous small nuclear groups along or just below mountain ridges in dense foliage on the tops and sides of the trees. In the Sierra Chincua, dozens of these small groups form along the major NW–SE ridge above the Arroyo La Plancha and its two northwestern extensions on both sides of the Arroyo El Zapatero.

This initial phase of colony formation is characterized by much movement and intense flight activity. We hypothesize that the presence of small groups along high ridges serves as a visual cue to attract more migrants to the roosts. Apparent signalling during this early part of the overwintering season may also occur through an additional and most remarkable behavior in which the butterflies form large towering spirals. We have seen these columns of soaring butterflies in early November extending vertically at least to the limits of 10× binoculars (300 m) above ridges and clearings near colonies which were in the process of formation.

The many small nuclear groups may move about and reform at other locations or coalesce with others, and by early November they are scattered along the ridges just below the crests for distances up to 3–4

FIG. 2. Trees coated with thick layer of rime and ice on a ridge above Chincua 6 (Colony 24, Table 1), 24 January 1981. The colony is located just outside photograph to the lower right. Exposed trees along the ridge are those on which first colony formation frequently takes place.

km. Movement continues into December and gradually the many smaller groups coalesce into a few (1–5) larger ones located further downslope, but always less than 200 m below the ridge crests. Fall migrants continue arriving during November and early December.

Consolidation into these larger groups continues through December with some colonies increasing in size at the expense of others. For example, during 1978/79, six groups were in the Chincua area on or before 6 December (Table 1). By early January, four had almost disappeared, and at least one of the two remaining ones had grown. During 1980–81, all five colonies at Chincua mapped in November had moved by 11 January from their positions on the upper slopes of Arroyo La Plancha to form a large (2.51 ha) colony lower down in the canyon (Table 1).

A major advantage of the movement of colonies from positions on high ridges to lower protected areas is the avoidance of the high altitude southwest winds and occasional storms that occur during the overwintering season (Mosino Aleman & Garcia 1973). This was dramatically illustrated in January 1981, when moisture-laden, gale-force winds covered the vegetation on an exposed ridge, where all of the groups had initially formed, with heavy ice and rime (Fig. 2). Note that the rime and ice did not form on trees in the protected valley below the ridge where the butterflies had established their colony. But even such sheltered butterflies can be dislodged by the tens of thousands from their roosts by high winds, rain, snow, or hail (Calvert et al. 1983). Once on the ground, they are subject to increased risk of mortality from freezing (Calvert & Brower 1981, Calvert & Cohen 1983) as well as mouse predation (Brower et al. 1985).

During the first phase of colony formation in November and December, the butterflies usually occupy only the outer periphery of tree branches, and rarely settle on trunks. However, by early to mid-January, they pack onto trunks and branches of the mid-sections of trees, avoid the upper quarters of crowns, and usually also avoid the lower branches. Packing into the interior branches and onto the trunks results in decreasing the total area occupied by the colony (Fig. 3a–c). On steeper slopes and for a short while after a colony has moved and resettled, clustering may occur on the lower branches as well. Clustering on trunks occurs in two ways. During normal weather, the butterflies form trunk and bough clusters in the same manner by flying up to a group of butterflies and landing. Following storms, the many thousands of dislodged individuals crawl up from the ground onto any vertical surface until they encounter butterflies or other obstacles. In this way they form the spectacular clusters which often extend nearly the full length of the trunk (Fig. 4).

Colony Location and Movement in Relation to Moisture Requirements

Overwintering in the high mountainous forests of the Transvolcanic Belt positions the colonies in a wetter habitat than that prevailing over much of Mexico during the winter. These conditions are due to a pattern of moist subtropical air masses that move east from the Pacific in late winter and early spring. When these air masses encounter the higher mountains west of the Continental Divide, adiabatic cooling results in cloud formation and precipitation, and a more even distribution of yearly precipitation than at lower elevations (Mosino Aleman & Garcia 1974, Anon. 1973: Landsat photo).

In years with ample rainfall, consolidation and movement cease by January. The colonies are typically located in protected habitats in a shallow, moist canyon along or near the headwater of a stream, where they remain until late February or March. Some colonies persist on mountain slopes unassociated with depressions, but almost without exception a source of water is located within less than 1 km.

Notwithstanding the wetter conditions at higher elevations where the colonies are located, long spells of dry weather do occur. During

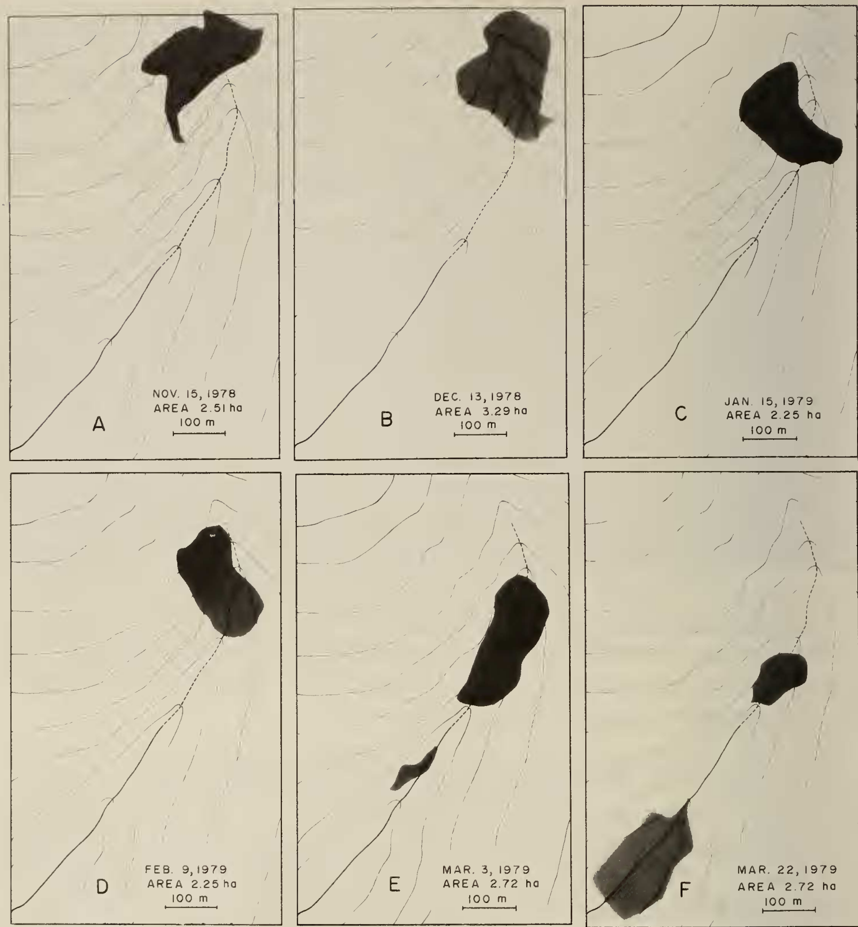

FIG. 3. Seasonal movement and size change of colony Chincua 4 from shortly after its formation in fall 1978 to its breakup in spring 1979. On 22 March a third fragment of the colony was 1 km downstream and is not shown in F. Contour interval = 20 m.

these times, tens of thousands of butterflies fly out of the colonies to drink in sunny areas along streams, moist patches or at reservoirs. Because of the distance of the colony from water, the butterflies must expend significant amounts of lipid (Chaplin & Wells 1982) in their watering flights. During exceptionally dry years, entire colonies may move downward and reform along or near water. For example, during 1979–80, when no rain occurred in the Sierra Chincua from 15 December to 9 February, three colonies located on the dry upper slopes of the Arroyo La Plancha moved about 0.5 km downslope (300 m elevation) during three weeks and reconsolidated into a single colony at the juncture of two streams (Colony 17, Table 1).

In addition to these occasional large-scale movements down to moister and more sheltered areas, colonies move incrementally or "creep" downslope during overwintering. This is explained as follows: On sunny days the thousands of butterflies that fly out of the colony return later the same day and reform their clusters on those portions of the lower colony periphery exposed to the sun. During winter afternoons, when most return, this is the southwest side. Cluster reformation occurs on the lower side of the colony because this part is usually closest to the water source. The net effect is a slow movement of the colony downslope, or down canyon, depending on where the parent colony is located. During periods of warm weather, when greater numbers travel out to water each day, this downslope creep can be rapid.

The relation of the butterflies' return route from water to the direction of colony movement was made clear in one notable exception to the above pattern. On 14 February 1978, a small, new segment of Colony 4 (Table 1) was located upslope 25 m northeast of the previously mapped colony. Instead of returning to the colony directly from the water source located to the south at the base of the mountain, some butterflies circled around the mountain and returned over the top from the northeast. As they approached the old colony, these butterflies reformed clusters on trees upslope from the old colony, and, as in the other instances, on branches exposed to the afternoon sun. Thus, the path of return from water seems to be the principal factor determining the direction of the incremental type of colony movement.

Colony Breakup

Due to seasonal warming in late February and March (Fig. 5), butterfly activity increases, and the colonies begin to reverse the consolidation process as larger and larger numbers fly out to water and nectar sources. The increasing daily efflux results in an acceleration of downslope or down-canyon movement. Often the colony splits into two or more parts as the butterflies returning from daily activities reform clusters nearer water or nectar (Fig. 3d–f). As occurs when they first arrive in November, new clusters form on the periphery of branches, while interior branches and trunks are largely avoided, resulting in a lower density but an increase in the total area occupied by the colony (Fig. 3e–f). After mid-March, colony size decreases as the butterflies start their remigration northward.

The Formation and Breakup of a Colony—a Case Study

The most detailed studies of the overwintering butterflies have been conducted near Site Alpha (Brower et al. 1977), located in what we now call the Chincua overwintering area. The Chincua Area is located at 19°41′N and 100°17–18′W in the Sierra Chincua 5–7 km NNW of

FIG. 4. Packing of monarch butterflies on trunks of the oyamel fir (*Abies religiosa*) is especially noticeable after winter storms when butterflies dislodged from their clusters by storm action crawl up the trunks.

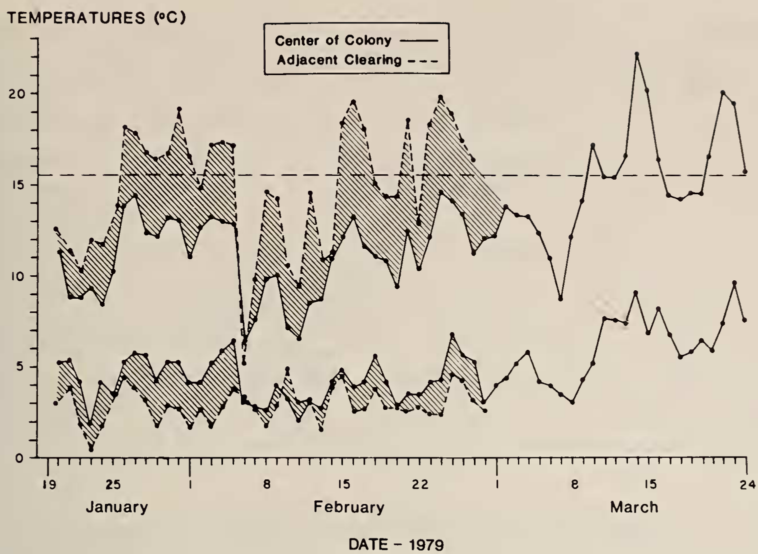

FIG. 5. Daily minimum and maximum temperatures as measured by one thermograph beneath the forest canopy in the center of a Chincua colony (Colony 10, Table 1) from 19 January–24 March 1979 (dashed lines), and another in a nearby clearing, from 19 January–28 February (solid lines). Horizontal dashed line is at 15.5°C, the approximate temperature at which monarchs are able to raise their thoracic muscles to flight temperature by shivering.

the town of Angangueo, Michoacan (Anon. 1976a: topographic map). The terrain is dominated by a SE–NW ridge of the Sierra Chincua, which drops from 3300 m to 2600 m elevation in its 6.3 km length, and is centered on a local landmark known as the Mojonera Alta ("high dividing line," Santamaria 1974). To the south, the ridge falls off steeply into the deep canyon of Arroyo La Plancha (also known locally as the Arroyo Hondo). The north slope of the Sierra Chincua is dissected by canyons that drain northwesterly. At its western end, the ridge divides forming the eastern and western sides of the westernmost of these canyons, Arroyo El Zapatero. Here butterfly colonies formed in seven of the past ten years, from 1976/1977 through 1985/1986.

We monitored the formation, consolidation, and breakup of one of these colonies (colony 10, Table 1) during the 1978–79 overwintering season (Fig. 3). When located on 15 November it was on the SW-facing slope (230°) of the head waters of Arroyo El Zapatero, approximately 140 m from the ridge crest and 180 m from the canyon bottom (Fig. 3a). At this time, the colony was still in the aggregation phase, and occupied 2.51 ha. By 13 December (Fig. 3b), it had moved downslope approximately 70 m and occupied 3.29 ha, the largest area it would attain. By 15 January (Fig. 3c), it had moved 110 m downward and westward. Due to increased packing on trunks and the interior parts of branches, it had consolidated to 2.25 ha. On 9 February (Fig. 3d) its size had not changed, but it had moved slightly westward (20 m) with its lower and upper boundaries remaining fixed. We mapped the colony again on 3 March (Fig. 3e), by which time the butterflies were very active. The colony had split into two parts and had spread out along Arroyo El Zapatero. It now occupied a total of 2.72 ha and was located 140 m west of its February position. We mapped the colony the last time on 22 March. By then it had spread out over 1 km of the canyon, occupied 3.2 ha, and consisted of two adjacent groups (Fig. 3f) and a third group farther downstream. On 15 April, walking the entire length of Arroyo El Zapatero, we encountered only one live butterfly where less than a month before there had been tens of millions.

Colony Location in Relation to Slope Exposure

The distribution of facing azimuths of the colonies is shown in the circular diagram (Fig. 6). The mean vector was 230°18′ with a 95% angular confidence interval of ±28°. Sixty-seven percent of the colonies formed on slopes in the SW quadrant, which shows a clear preference of the butterflies for this quadrant ($r = 0.56$, $P < 0.001$). Of the nine colonies that formed on slopes facing other directions, two were located just to the east, and in the lee of, a SW-facing ridge (Colonies 1 and 2, Table 1), five were located in canyons that drained to the west (Colonies 3, 5, 25, 27 and 28) and the remaining two formed on slopes facing SSE, one very close to the SW quadrant (Colonies 22 and 30). One colony formed initially on a SSE slope and later moved around to a slope in the SW quadrant (Colony 8).

During the winter in mountainous areas, southern slopes receive more insolation and dry faster than northern ones. Moreover, SW slopes are heated more than SE ones because, when the sun strikes the eastern slope in the morning, much of its energy is spent in evaporating water that precipitated as dew during the night. In contrast, the afternoon sun strikes relatively dry ground, so most of its energy is spent in heating the surface (Geiger 1950). In spite of a strong need for the butterflies to stay cool, conserve fuel, and avoid desiccation, they appear to choose the hottest and driest slopes available. This apparent contradiction needs explanation.

We hypothesize that their location on SW-facing slopes is a compromise that satisfies several requirements. During mid-winter days, air temperatures within the shade of the oyamel forests rarely become warm enough for monarchs to fly spontaneously. The minimum am-

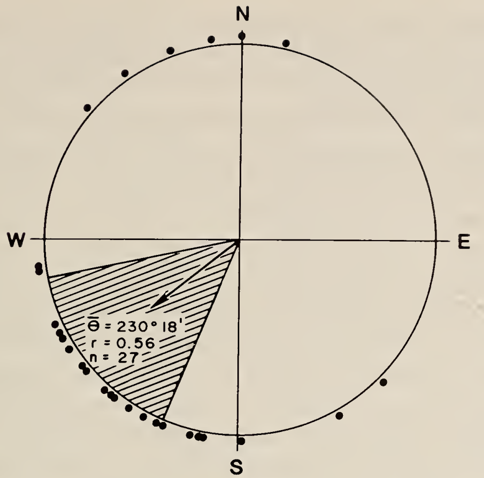

FIG. 6. Direction of the slopes (faing azimuths) on which 27 monarch butterfly colonies were located in Mexico's Transvolcanic Belt, 1976–82. Shaded area is angular confidence interval.

bient temperature at which monarchs can shiver and then fly is between 12.7 and 16°C (Kammer 1970, Masters 1985). Air temperatures of this magnitude were not reached in shaded portions of the 1978–79 Chincua 4 colony until March 9 (Fig. 5). Even though temperatures are below flight threshold within the colony during most of the overwintering season, direct solar radiation usually reaches the butterflies as sun flecks at some time during clear or partly cloudy days. This allows them to warm to flight threshold by basking so they can regain their positions in the trees after being knocked down by storms, and also insures that they can fly out to water and nectar on clear days. In addition, their basking posture readily displays their aposematic coloration and helps to deter bird predators, which killed an average of 15,000 butterflies/day during 1978–79 (Brower & Calvert 1985). This same study showed that predation is inversely related to temperature and suggests that the birds would have an even greater advantage on the colder, north-facing slopes. Although a position on the north-facing slope would be better for maintaining water balance and conserving lipids, the colder temperatures would result in greater inactivity so that the butterflies would be less able to redress an unfavorable water balance, reestablish colony integrity after storms, avoid predators, and obtain nectar.

The Importance of Slope Inclination

Surface heating of mountainous areas depends on the amount of radiation striking slopes. While several factors including season, time of day, latitude, and the facing direction of slope affect radiation, the degree of slope is critical. Schubert (in Geiger 1950) showed that during winter, a south slope inclined at 23.5° receives 9% more heat than a horizontal one. The inclination of the slopes on which the butterfly colonies are situated averaged 25°22′ with a 95% angular confidence interval of 1° (Table 1). Butterflies roosting here would receive more solar energy to warm them, and their ability to fly would thus be enhanced.

Moreover, surface heating due to solar radiation striking near the perpendicular to the mountainous slopes occupied by the colonies is maximal on about 1 March. This coincides well with the date that the butterflies begin to accelerate flight activity and mating, and move down the canyons in preparation for their remigration to the north. The reason for this early March maximum is as follows: At the latitude of the overwintering colonies (ca. 19.5°N), the date when the sun's rays are exactly perpendicular to the average colony slope (25°22′ = approximately 25.4°) is 1 March. At the spring equinox, the angle of incidence of the sun at the latitude of the colonies is 95.5°. This value is obtained by adding the average slope inclination (25.4°) to the angle of incidence of the sun's rays to the horizontal [25.4° + (90° − 19.5)] = 95.9°. Therefore, at solar noon on 22 March, the sun is 5.9° beyond the perpendicular to the average colony slope. Since the earth precesses at a rate of 0.2575°/day, it takes about 23 days (5.9°/0.2575°/day = 22.9 days) to reach this position. Therefore, the sun's rays were perpendicular to the colony slopes about 1 March.

Why Do Monarchs Migrate to Mexico's Transvolcanic Belt?

Evidence that monarchs are not sufficiently cold-tolerant to survive winter conditions in their northern breeding areas derives from several sources. Urquhart (1960) found that 77% of monarch pupae subjected to freezing temperatures associated with a cold front perished. Calvert and Brower (1981) showed that 60% of monarchs wetted by naturally occurring dewfall in a clearing near a Sierra Chincua colony suffered flight impairment or death after one night's exposure to temperatures averaging only −1.7°C. Moreover, during January, 1981 within a Sierra Chincua colony (Colony 24, Table 1) inclement weather with low temperatures reaching −5°C resulted in the death of an estimated 2.5 million butterflies (Calvert et al. 1983). Anderson (in Brower, in press) found in a controlled freezing chamber that the temperature at which 50% of the dry and wet monarchs freeze from a Chincua colony is −7.8°C and −4.4°C, respectively. Calvert et al. (in press) found in the same area that the temperature at which 50% of monarchs wetted by nighttime dewfall in the open forest freeze or are injured to the point where they could not fly normally is −3.1°C. Thus, temperatures slightly below freezing kill or incapacitate monarch butterflies, necessitating their migration from their northern breeding grounds. An additional reason for migrating southward is the senescence of their larval food plants. However, if the monarchs could survive the cold, they could, presumably, overwinter in the north as do other adult butterflies such as the mourning cloak (*Nymphalis antiopa* L.).

The monarchs' need to avoid lethally cold temperatures must be balanced against their need for moderate cold to avoid too rapid depletion of their lipid reserves (Tuskes & Brower 1978, Chaplin & Wells 1982, Brower 1985, Walford & Brower, in prep.). Long-term minimum temperature records (10–29 years) for November through March at seven meteorological stations above 2500 m located near the overwintering colonies averaged 2.3°C (Anon. 1976b). The average minimum, average maximum and mean temperatures for a 40-day period (19 January–28 February 1979) in a clearing 20 m outside a Sierra Chincua colony (24, Table 10) were 2.9°, 14.9°, and 8.9°C (Fig. 5; also Brower & Calvert 1985). The overwintering areas are thus located at an altitude and latitude that normally provide a cool environment with relatively stable minima at or just above freezing.

The dense forests of the Transvolcanic Belt also play an important role in moderating the climate by reducing daily temperature extremes. Thus, inside the center of the colony for the same 40-day period described above, the average minimum temperature was higher (4.2°) while the average maximum and mean temperatures (11.0° and 7.7°) were lower than the corresponding averages in the nearby clearing (compare Fig. 5). The moderating effect of the forest cover becomes crucially important for monarch survival when temperatures plummet to the killing threshold (Calvert et al. 1983).

Latitudinally, the monarch's choice of colony location may be limited by two physical barriers. Immediately south of the Transvolcanic Belt lies the Balsas River depression (Fig. 1). Here the hot, dry climate would undoubtedly break their reproductive diapause (Baker & Herman 1976), and cause them to begin ovipositing in areas already occupied by indigenous milkweed butterflies, *Danaus gilippus* L. and *D. eresimus* Cramer, as well as nonmigratory monarchs (Calvert, unpubl. obs., Brower 1985). To the north lie the dry plains of the Central Plateau where in winter the butterflies would be subjected to colder and drier conditions brought about by the influence of advective air masses moving down from the north (Zepeda 1941, Mosino Aleman & Garcia 1973). In this thinly forested region they would also not have the protective cover and microclimatic requisites provided by the dense forests of the Transvolcanic Belt. Suitable habitats may exist further south in Mexico and Guatemala, but areas above 3000 m are more limited in extent and lack the extensive fir forests found in the Transvolcanic Belt (Calvert & de la Maza, unpubl. obs., Anon. 1981: distribution of oyamel forests).

The conflicting requirements to avoid freezing temperatures and yet remain relatively cool, and to avoid excessive moisture that raises the temperature at which freezing injury occurs, and yet to remain relatively moist to avoid desiccation are closely approximated in the oyamel forest ecosystem at the geographic location between 19 and 20°N in Mexico's Transvolcanic Belt.

The monarchs' return to the north is also bounded by several constraints. It must not precede the flush of spring milkweeds and the recession of lethally cold, late winter temperatures. And finally, it must allow for the first spring generation, largely produced in the Gulf Coastal States (Brower et al., in prep.) to mature before the advent of lethally warm summer temperatures in the southern United States (Malcolm et al. 1987).

CONCLUSIONS

Monarch migration to and colonization of high altitude tropical areas in Mexico appear to be an adaptive response to several temperature- and water-related needs. Flight capacity is necessary to regain position in clusters following storms, to avoid predators, to locate nectar sources, and, especially, to obtain water. Direct and indirect solar radiation augmented by a SW exposure and favorable slope inclination allow the butterflies to warm sufficiently to fly when temperatures within the forest are below flight threshold. However, warming and flying in the course of daily activities increases their utilization of precious lipid reserves. The generally cool climate with sufficiently intense sunshine to allow flight appears to satisfy both their need to conserve energy and fly out of the colony when necessary. The location of the mountains is far enough south to minimize the impact of most cold air masses, which dominate winter weather in the north. Nighttime minima, which seldom drop more than a few degrees below freezing except during occasional extreme cold periods, reduce the likelihood of death by freezing. These often conflicting requirements are approximately satisfied by the unique climatic and physiographic features of Mexico's Transvolcanic Belt.

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